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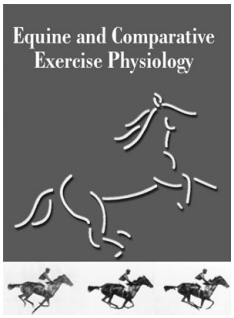


# Segmental variation in the activity and function of the equine *longissimus dorsi* muscle during walk and trot

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## Abstract

Muscle function depends in part on the interplay between its activity and its length within the stretch-shortening cycle. The *longissimus dorsi* is a large epaxial muscle running along the thoracic and lumbar regions of the equine back. Due to its anatomical positioning, the *longissimus dorsi* has the capability of contributing to many functions: developing bending moments in the dorsoventral and lateral (coupled to axial rotation) directions and also providing stiffness to limit motion in these directions. We hypothesize that the exact function of the *longissimus dorsi* will vary along the back and between gaits as the relation between activity and motion of the back changes. Electromyograms (EMG) were recorded at walk (inclined and level) and trot (on the level) on a treadmill from the *longissimus dorsi* at muscle segments T14, T16, T18 and L2. Back motion was additionally measured using a fibre-optic goniometer. Co-contractions of the muscle between its left and right sides were quantified using correlation analysis. A greater dominance of unilateral activity was found at more cranial segments and for level walking, suggesting a greater role of the *longissimus dorsi* in developing lateral bending moments. Timing of the EMG varied between muscle segments relative to the gait cycle, the locomotor condition tested and the flexion–extension cycle of the back. This supports the hypothesis that the function of the *longissimus dorsi* changes along the back and between gaits.

**Keywords:** equine; EMG; flexion; back; *longissimus dorsi*

## Introduction

The *longissimus dorsi* is the largest muscle in the equine back and extends along the entire thoracic (T) and lumber (L) regions. It is an epaxial muscle that is situated dorsal to the transverse spinous processes and lateral to the dorsal spinous processes. Based on its gross anatomical positioning, the function of the *longissimus dorsi* has been described as being capable of providing extension when bilaterally active, and lateral bending and axial rotation to the spine when unilaterally active[1]. During walking around tight turns, there is a strong unilateral activity on the ipsilateral side to the centre of the turn[2], illustrating a role of this muscle in lateral flexion. Additionally, the *longissimus dorsi* has been attributed to limiting dorsoventral movements at trot, i.e. providing stiffness[3,4]. However, during locomotion, the mechanical function of a muscle depends on the interplay between its activity and the stretch-shortening cycle of its muscle fascicles. The *longissimus dorsi* is segmentally innervated[1], leading to potentially different activation times in the different muscle segments. The stretch-shortening cycle of the fascicles depends on both the range of motion of the back that varies between gaits and along the back[3–6] and the anatomical positioning of the muscle and the three-dimensional orientation of the fascicles within the muscle belly; these parameters are largely unreported. It is thus likely that the mechanical function varies between different regions

of the muscle and may also vary across different locomotor tasks.

Studies on back stiffness have shown that *in vivo* stiffness[7] can be substantially greater than the stiffness in cadaveric backs[8], presumably due to the action of muscle activity that in turn increases the muscle stiffness. The muscle provides greater stiffness to the back in the lateral than in the dorsoventral direction[7], and this is presumably due to its greater moment arms and mechanical advantage in the lateral direction (as seen in images in Haussler[1]). Stiffness may be developed by a muscle in order to increase stability and to limit the motion that occurs in reaction to externally applied forces. The stiffness developed by the equine *longissimus dorsi* depends on both the size of the muscle at different segmental positions and its level of activity. It is thus likely that the role of the *longissimus dorsi* in providing stiffness to the back varies at different segmental positions and for different locomotor tasks.

When a muscle develops force, it generates moments about the joints across which it acts. Due to its anatomical positioning, the *longissimus dorsi* can generate moments in the dorsoventral, lateral and axial rotation directions[1]. The moments generated by the muscle will potentially vary along the back as the cross-sectional area and activity levels change, and will also vary in the different directions due to the different moment arms that result from its anatomical positioning. We can make predictions about the role of the *longissimus dorsi* in generating bending moments and stiffness on the back based on the levels of muscle activity: bilateral activity will result in increased stiffness and a net extensor moment in the dorsoventral direction, whereas unilateral activity will result in increased stiffness and a net lateral bending moment. We will thus be able to assess changes in muscle function by examining the relative phases of activity between the left and right sides.

In order to make such an analysis, it is necessary to record the activity of the muscle from multiple segments and to simultaneously compare these activities with measurements of the back kinematics. The purpose of this study was to describe the relative levels and phase relations of the electromyograms (EMGs) from the *longissimus dorsi* at four different muscle positions: T14, T16, T18 and L2. We compared these EMGs with the motion of the back during treadmill locomotion at different speeds, gaits and inclinations in order to test the hypothesis that the function of the *longissimus dorsi* varies between muscle segments and between different locomotor conditions.

## Methods

### *Horses*

Five geldings and one mare were used in this study (height at withers $1.55 \pm 0.01$ m; age $9 \pm 2$ years). The horses were initially assessed by a veterinary surgeon to ensure that they were fit to participate in the study. Their owners provided signed and informed consent.

Each horse was tested over the same protocol. Kinematic and electromyographic measurements were taken as described below. Initially, measurements were recorded during 2 min of standing straight with all four feet weighted and the head loosely held at a neutral height. Measurements were then recorded for 2-min periods during a series of treadmill tasks presented in the following order: (1) slow walk ($1.47\,m\,s^{-1}$), (2) fast walk ($1.80\,m\,s^{-1}$), (3) slower trot ($2.62\,m\,s^{-1}$), (4) faster trot ($3.83\,m\,s^{-1}$), (5) faster trot, (6) slower trot, (7) fast walk, (8) slow walk. All these tests were performed on the level. The following measurements were then recorded for 2-min periods: (9) walk at 5° incline, (10) walk at 10° incline, (11) walk at 10° incline, (12) walk at 5° incline. All these tests were performed at a slow walking speed. The slow and fast speeds were kept the same for all tests for each gait, but were adjusted for each horse. The data collection finally concluded with measurements during 2 min of standing straight with all four feet weighted and the head loosely held at a neutral height.

### *Muscle activity*

Muscle activity was measured using eight bipolar Ag/AgCl EMG electrodes (10 mm in diameter, 30 mm spacing) adhered to the skin overlying the left and right sides of the *longissimus dorsi*. Prior to electrode placement, the skin was prepared by clipping, shaving and cleaning with isopropyl alcohol. A series of post-mortem dissections on cadaver backs had shown that the *trapezius* muscle is more superficial to the *longissimus dorsi* at sites more cranial to L14, and the *gluteus medius* is more superficial at sites more caudal to L2, therefore surface EMG can only reliably be measured between T14 and L2. Electrodes were placed bilaterally, adjacent to the dorsal spinous process of the T14, T16, T18 and L2 vertebral segments. The electrodes were arranged on a path 12 cm to the midline at T14 to 8 cm from the midline at L2 in order to minimize crosstalk from adjacent muscles. A ground electrode was placed over the bony prominence of the *tuber sacrale*. The EMG was preamplified 5000 times (Biovision, Werheim, Germany) and sent to the multiplexing unit on the surcingle. The electrodes and associated cables were taped to the hair to minimize artefacts from cable movement. Additionally, the time of left hind foot contact within each stride was identified by the rapid deceleration recorded using a uniaxial accelerometer that was attached to the cranial aspect of the hoof using hot glue.

The accelerometer was connected via a cable to a multiplexing unit on the surcingle.

### *Back motion*

The back motion was measured using a fibre-optic goniometer (Shapetape, Measurand Inc.). The goniometer in its protective sheath ran through a series of custom-made leather guides that were fixed to the top of the back using hair extension adhesive. The sheath was rigidly fixed within the guide that was attached over spinous process of the L1 vertebrae and was used as a reference point on the cable. The fibre-optic cables had a 1 m active region that sensed position: 32 channels of bend and twist data were generated corresponding to 62.5 mm segments along the goniometer, and these were sent as analog voltage signals to a multiplexer unit on the surcingle.

### *Data collection*

Signals from the footfall accelerometer, EMG and back motion were conditioned on a custom-made multiplexer unit attached to the surcingle and subsequently recorded on a notebook computer placed on a table (16-bit data acquisition card, 6036E, National Instruments, TX, USA) via a shielded cable. A 2 kHz clock source from the computer was used to synchronize all channels of data collection. Data were recorded at 2000 Hz for the footfall accelerometer and EMG and 62.5 Hz for the fibre-optic channels. Data were collected in a LabVIEW programming environment (National Instruments).

### *Data analysis*

The recorded EMG signals contained a large component of interference from the electrocardiogram (ECG) that was removed using a cross-correlation and subtraction technique[2,9]. Briefly, the shape of the ECG was identified for each recording site from the recordings of the standing trials where there was very little EMG activity present. This was cross-correlated with the movement EMGs to identify the time of each heartbeat and subsequently subtracted from the raw traces during the movement trials to yield the 'clean EMG' signal.

The intensity of the EMG was calculated using an EMG-specific wavelet analysis[10,11]. Briefly, the intensity is a close approximation to the power of the EMG and is visualized as a positive envelope that describes the timing and magnitude of the signal. The intensities were initially calculated across a range of frequency bands (wavelet domains[10] 2–10: frequency band 24–380 Hz), and the total intensity calculated as the sum of the intensities across these frequencies. By filtering out the low frequencies ($< 24$ Hz), this process removed both movement artefacts and residual noise from the ECG[9]. The total intensity was calculated for the clean EMG signal interpolated to 100 points for each stride delimited by the foot contact time from the left hind foot. The coordination of the EMG activity between the left and right sides was estimated by correlating the total intensity trace for one recording site with the same trace phase-shifted by 50% of the gait cycle. The phase relations of the total intensity traces at different regions were calculated with shift registration using the Procrustes method[12].

Back-motion data from the fibre-optic goniometer were demultiplexed and the mean signal for each channel was interpolated into 100 points per stride. These data were converted to three-dimensional position and orientation data for the 16 segments along the cable (Shapeware, Measurand Inc., Canada). It was assumed that the fixed point of the fibre-optic cables at L1 was aligned to the sagittal plane: $x$-axis cranial, $y$-axis lateral and $z$-axis dorsal. The geometry of the goniometer was resolved into components in the dorsoventral and lateral directions and calculated at the position of segments T14, T16, T18 and L2. The mean geometry of the goniometer during the standing trials was subtracted from the moving trials to yield the changes in back position that occurred during locomotion, and these were expressed as curvatures (curvature = 1/radius of curvature) in the dorsoventral and lateral planes. The phase relations of the back curvatures at different regions were calculated with shift registration using the Procrustes method[12]. Data analysis was performed in a Mathematica programming environment (Wolfram Research Ltd, Long Hanborough, UK).

General linear model analyses of variance were used to determine the effect of different factors on the EMG intensity, EMG correlations, EMG- and curvature-phase relations (Minitab Inc., State College, PA, USA). Horse, locomotor condition, muscle segment and a segment–condition interaction term were used as factors in each test. Additionally, a term was used to distinguish dorsoventral from lateral curvature-phase values for the kinematic test. Tukey *post hoc* tests were used to determine significant differences between subgroups of the data and all tests were considered significant at the $\alpha = 0.05$ level. Within each test, the least-squares mean values were calculated for the main effects (locomotor condition and muscle segment) and these were plotted in the figures. Values are reported as mean ± SEM.

## Results

Data were analysed for a total of 9043 strides. The mean velocities and stride durations used for the different conditions are shown in Table 1. There was a significant decrease in stride duration as the velocity increased, but there was no significant difference between stride durations for the three conditions

**Table 1** Gait parameters for the six conditions tested. Values are shown as mean ± SEM

| Condition | Velocity ($m\,s^{-1}$) | Stride duration (s) | Number of strides |
|---|---|---|---|
| Walk, slow at 0° | 1.47 ± 0.02 | 1.08 ± 0.01 | 1440 |
| Walk, fast at 0° | 1.80 ± 0.00 | 0.97 ± 0.01 | 1356 |
| Walk, slow at 5° | 1.47 ± 0.02 | 1.12 ± 0.01 | 1071 |
| Walk, slow at 10° | 1.47 ± 0.02 | 1.11 ± 0.01 | 1270 |
| Trot, slower at 0° | 2.62 ± 0.10 | 0.76 ± 0.01 | 1796 |
| Trot, faster at 0° | 3.83 ± 0.03 | 0.68 ± 0.01 | 2110 |

at slow walk: level, 5° and 10° (one-way ANOVA *post hoc* test).

Sample EMG traces are shown for one horse in Fig. 1 for three of the locomotor conditions. This figure illustrates how the EMG intensity increased between the slow walk, through walk up the incline to the faster trot. In each of these conditions, there were two major periods of activity in the *longissimus dorsi*, occurring at the end of each half-gait cycle. Points of particular note are that the relative level of EMG intensity changed between the muscle segments, with the intensity decreasing from T14 to L2 at 65% stride in the slow walk (Fig. 1a) and the intensity increasing from T14 to L2 at 40% stride in the faster trot (Fig. 1c). Additionally, the timing of EMG onset and offset varied between the muscle segments: L2 onset was in advance of T14 between 70 and 80% stride in the incline walk (Fig. 1b) and T14 offset was in advance of L2 between 40 and 50% stride in the faster trot (Fig. 1c). A complete set of EMG data for all horses was obtained only from the right *longissimus dorsi*, and these data were used for further analysis. The pooled results are described below.

There was a significant effect of locomotor condition on the EMG intensity (Fig. 2). *Post hoc* tests showed that the EMG intensity for the two level-walking conditions was not significantly different between the two and the EMG intensity for the trotting conditions was not significantly different between the two. The trotting conditions had a significantly higher EMG intensity than the level-walking conditions. The EMG intensity for walking up a 10° incline was significantly higher than the level walking and not significantly different from the $2.5\,m\,s^{-1}$ trot. There was a 38% decrease in EMG intensity between muscle segments T18 and L2; however, *post hoc* testing showed that this effect was not significant ($p = 0.059$). The interaction term between the locomotor condition and muscle segment had no significant effect on the EMG intensities.

There were significant effects of both the locomotor condition and the muscle segment on the EMG correlation values (Fig. 3). The EMG correlations for the two level-walking conditions were significantly less than those for the other more demanding conditions. *Post hoc* tests showed that the EMG correlations for the two trotting conditions were not significantly different from each other, and the EMG correlation for the slower trot at $2.6\,m\,s^{-1}$ was significantly higher than that for any of the walking trials. The EMG correlation increased in a cranial–caudal direction from the muscle segments T14 to L2. The EMG correlation at T14 was significantly lower than at the more caudal segments, and that at L2 was significantly higher than at the more cranial segments. The interaction between the locomotor condition and muscle segment had no significant effect on the EMG correlation values.

There were significant effects of both the locomotor condition and the muscle segment on the EMG-phase relations (Fig. 4). The EMG phase was significantly higher for walking at a 10° incline than for the other walking conditions. The 10° incline walking and slower trot at $2.6\,m\,s^{-1}$ had EMG phases not significantly different from each other, but their values were significantly higher than the other conditions. The EMG phase was significantly different between the segments T14, T16 and T18. The EMG phase was not significantly different between the T16 and L2 segments. On average, the EMG phase changed by 16.3 m s between muscle segments T14 and T18. The interaction between the locomotor condition and muscle segment had a significant effect on the EMG-phase relations, showing that the manner in which the EMG phase varied between muscle segments was dependent on the locomotor condition.

There was no significant effect of the direction (lateral *versus* dorsoventral) on the curvature-phase relations. There were significant effects of both the locomotor condition and the muscle segment on the curvature-phase relations (Fig. 5): there was no significant difference in the curvature phases between segments T14 and L2; however, curvatures at segments T14 and L2 both occurred significantly before those at T18. The curvature phases were not significantly different from each other for the walking and the trotting conditions. Curvatures for the faster trot at $3.8\,m\,s^{-1}$ occurred significantly before those for the walking conditions. The interaction between the locomotor condition and muscle segment had a significant effect on the curvature-phase relations, showing that the manner in which the curvature phase varied between muscle segments was dependent on the locomotor condition. The relative differences between the EMG- and curvature-phase relations can be seen in Fig. 5. ANOVA showed that there was a significant difference in the EMG- to curvature-phase relations between muscle segments T18 and L2.

## Discussion

The major feature of the EMG intensity was for two bursts of activity within each stride (Fig. 1). This

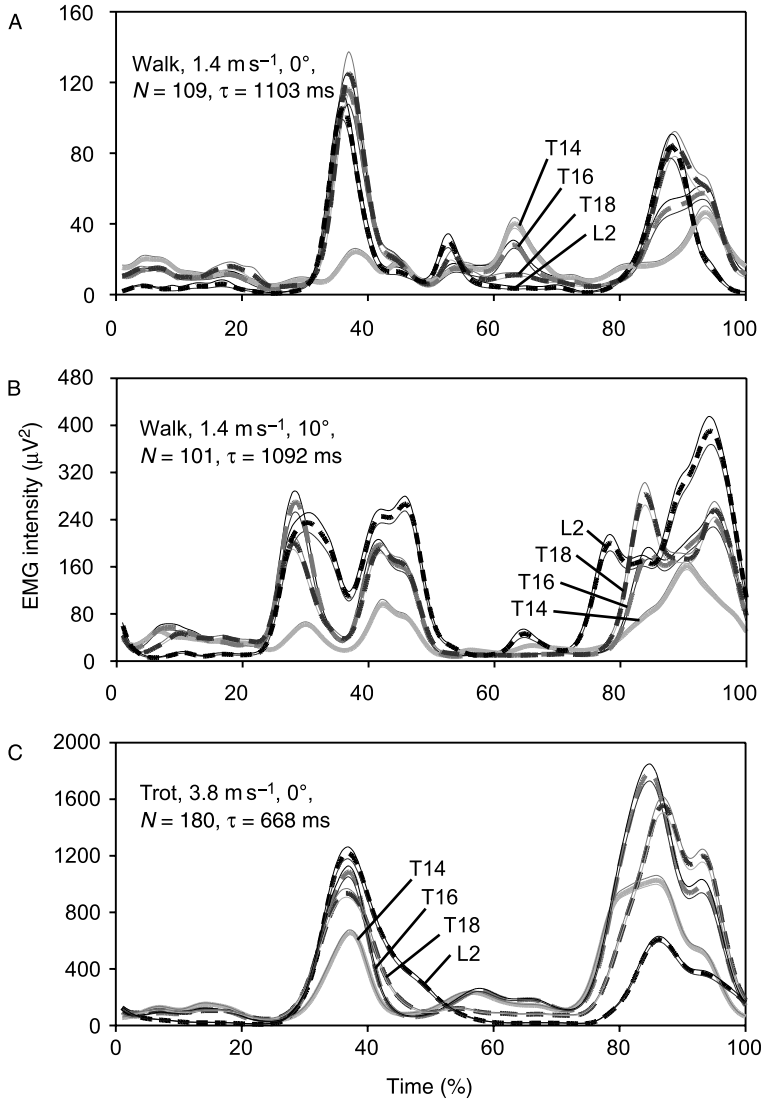


**Fig. 1** EMG intensities at different muscle segments in the right longissimus dorsi during walk and trot for one horse. Thick lines show the mean EMG intensity for each segment T14, T16, T18 and L2, and are graded from solid, light grey for T14 to dashed, black for L2. Thin lines show the SEM. The time axis is normalized to one gait cycle starting and finishing at the time of ground contact of the left hind foot. Text in each plot indicates the gait, velocity, inclination, number of strides analysed and the stride duration $\tau$

general pattern of activity is consistent with previous reports of trot[4,13–15] but now shows that similar patterns also occur during walk. The example in Fig. 1 shows how the duration of each burst of activity is increased for trot and incline walking compared with level walking, and additionally the timing of these bursts relative to the stride also varies. Previous studies on the EMG activity at L3 have shown that each burst of activity starts and finishes later when inclination is increased at trot, and also each burst starts earlier and ends earlier when the speed of trot is increased[13]. These combined effects resulted in no significant difference in the duration of each burst of EMG across the range of trotting speeds[14]. In this study, we show that the actual timing parameters additionally vary along the *longissimus dorsi*, and therefore it is important to quantify the EMG at different segments if the function of the muscle in its different regions is to be evaluated.

Only one previous study has reported the EMG from different sites of the *longissimus dorsi* during locomotion in the horse[15], and it was reported that the level of EMG in the *longissimus dorsi* was decreased between muscle segments T12, through T16 to L3 at trot. We are unable to statistically support such observations with the data in this study (Fig. 2). The presence of ECG artefact at the recording electrodes can artificially increase the recorded levels of activity[2], particularly in the more cranial segments. In this study, we have used a combination of ECG subtraction and high-pass filtering to minimize such ECG artefact[9]: comparisons between studies should always consider the extent to which the ECG has been eliminated. Normalization to a standard horse- and muscle-specific

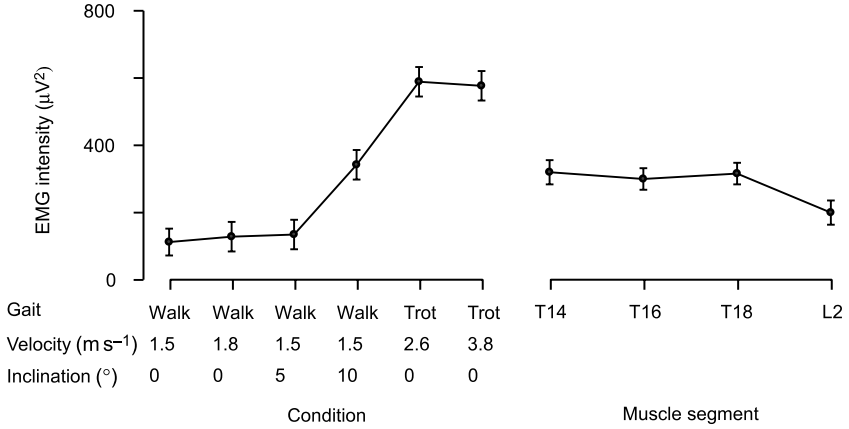


**Fig. 2** Main effects plot for EMG intensity along the longissimus dorsi for different locomotor conditions and muscle segments. Data from all horses, conditions and segments were used in the ANOVA: the panels show the main effect of the condition or muscle segment, respectively, averaged across the levels of the other factors. Symbols show the mean ± SEM. EMG intensity for each gait cycle

level is a common procedure in EMG analysis and can improve the power of statistical testing. However, in order to make comparisons of the level of EMG between the different recording sites on the different muscle segments, it was necessary to compare the absolute values of EMG without prior normalization. Decreases in EMG intensity between T14 and L2 were noted, but were not statistically significant. The EMG intensity significantly increased with inclination at walk, and this is consistent with increases reported for increased inclination at trot[13]. We did not find any significant effect of speed on the EMG intensity for either walk or trot; however, it has been reported that EMG does increase with speed (over a range of 3.5–6.0 m s$^{-1}$) at trot[14]. It is possible that the range of speeds used in this study (Table 1) was not sufficient to reveal increases in EMG intensity for each gait.

Correlations of EMG intensity between the left and right sides allow interpretations to be drawn about the role of the muscle in generating dorsoventral and lateral bending moments. The intention of this study was to correlate the EMG from the left and right *longissimus dorsi*, but due to technical difficulties we obtained only a complete dataset for the right side of each horse. However, both walk and trot are symmetrical gaits, and we have made the assumption that the activity in the left *longissimus dorsi* mirrors that in the right *longissimus dorsi*, with a 50% phase shift (relative to the gait cycle). This assumption is supported by the reports that the EMG is 50% out of phase between the two sides of the *longissimus dorsi* at trot[15]. This allows us to assume that the contralateral EMG activity is the same as the ipsilateral activity shifted by half a gait cycle. Using this method, we have shown substantial and significant variations in correlation between locomotor conditions and between the muscle segments (Fig. 3). Higher correlations indicate more phasic activity between the left and right sides, and this would result in dorsoventral extensor moments dominating. Lower correlations indicate the EMG between the left and right sides as being more out of phase and

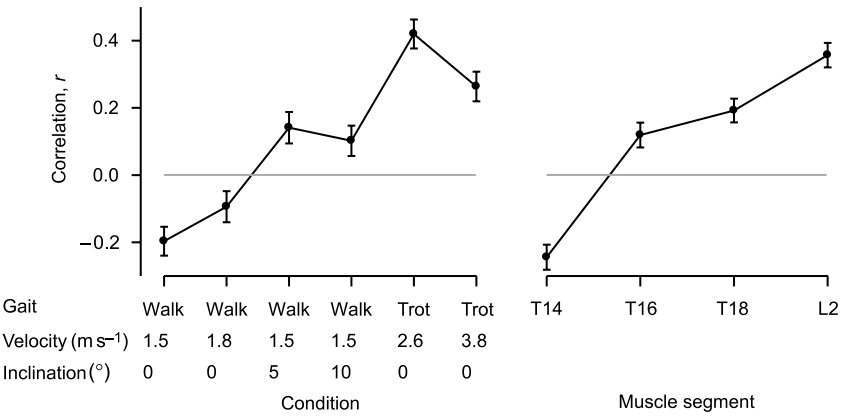


**Fig. 3** Main effects plot for EMG correlations between the left and right longissimus dorsi for different locomotor conditions and muscle segments. Data from all horses, conditions and segments were used in the ANOVA: the panels show the main effect of the condition or muscle segment, respectively, averaged across the levels of the other factors. Symbols show the mean ± SEM

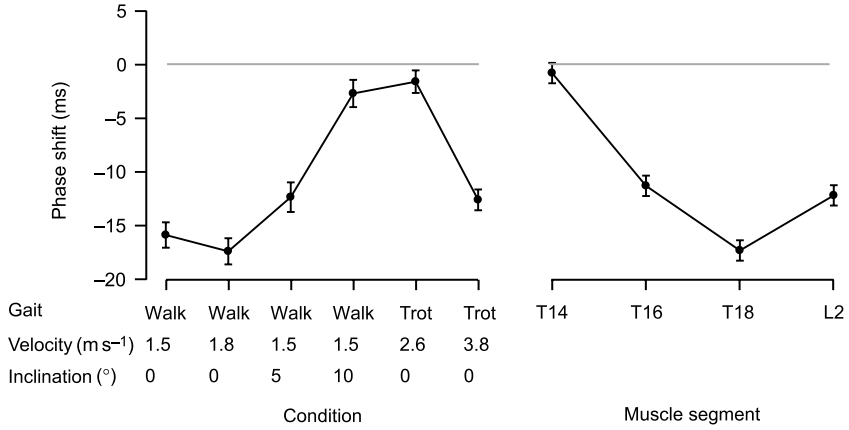


**Fig. 4** Main effects plot for EMG-phase relations for the longissimus dorsi for different locomotor conditions and muscle segments. Data from all horses, conditions and segments were used in the ANOVA: the panels show the main effect of the condition or muscle segment, respectively, averaged across the levels of the other factors. Symbols show the mean ± SEM. Earlier activation times are shown by more positive phase shifts

thus a greater role of developing lateral bending moments. It should be remembered that these correlation values are independent of the level of muscle activity and so do not indicate whether the muscle is active at all, and hence the correlation results should always be considered with the levels of EMG intensity in Fig. 2. It is interesting to note that the EMG intensity was similar for the two level-walking conditions and the walk at the 5° incline (Fig. 2); however, the least-squares mean correlation increased from $-0.20 \pm 0.04$ to $0.14 \pm 0.05$ across these conditions. These results demonstrate that the *longissimus dorsi* has a greater role in generating lateral bending moments for the less demanding walking conditions. Comparison of the least-squares mean correlations in EMG intensity between muscle segments shows a large increase from $-0.24 \pm 0.04$ at T14 to $0.36 \pm 0.04$ at L2 (Fig. 3), despite there being no significant difference in the EMG intensity (Fig. 2). These results demonstrate that the role of the *longissimus dorsi* for generating lateral bending moments is more dominant at the more cranial recording sites, and this is a general result across the range of walking and trotting conditions tested.

Muscle function can be broadly considered as eccentric, isometric or concentric depending on whether the periods of muscle activity occur during muscle fascicle lengthening, constant length or shortening, respectively. Eccentric contractions absorb mechanical work whereas concentric contractions generate mechanical work, and these in turn can indicate different mechanical roles of the muscle. The *in vivo* muscle fascicle strains depend on the complex interaction between the three-dimensional geometry of the muscle fascicles, their position relative to the joint centres of rotation and the *in vivo* joint rotations. Our kinematic data support previous studies which show that the vertebral rotations occur in dor-

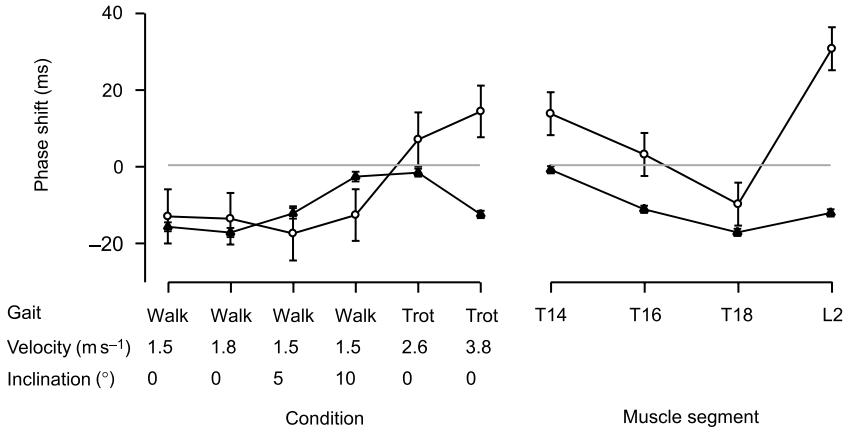


**Fig. 5** Main effects plot for curvature-phase relations for the equine back for different locomotor conditions and muscle segments. Back curvatures (mean ± SEM) are shown by the open circles and represent the pooled data for the dorsoventral and lateral directions. Data from all horses, conditions and segments were used in the ANOVA: the panels show the main effect of the condition or muscle segment, respectively, averaged across the levels of the other factors. The EMG-phase relations (squares) from Fig. 4 are shown for comparison

soventral, lateral and axial directions and furthermore vary between segments. However, there are currently no detailed three-dimensional architectural data available to allow the muscle fascicle strains to be calculated during locomotion. However, the magnitude of the phase differences for the back kinematics was greater than for the EMG intensities and so there was a change in the relative timing of the EMG intensity with the flexion–extension cycles between the different muscle segments. These results allow us to make the general conclusion that the muscle is active at different phases in the fascicle stretch–shortening cycles, leading to the development of different stress and mass-specific powers at the different muscle segments.

The registration analysis of the EMG intensity calculates the phase shift that would be required to align the EMG intensity traces from the different segments while minimizing their variation from the mean shape of an EMG intensity trace[12]. This procedure considers all the temporal information within each trace and outputs a phase number that defines the relative timing of the EMG intensity traces. The results are calculated relative to a consistent point in each gait cycle, which in this case is the left hind foot contact as measured by the accelerometer. The registration analysis showed significant variation in the EMG phases between muscle segments (Fig. 4). The results also showed that the relative phase relations between muscle segments also depended on the locomotor condition, and so these variations in the timing of EMG intensity must be the result of an active strategy by the central nervous system. The EMG intensity traces occur progressively later between T14, T16 and T18, but there is a break in this pattern when moving to the L site at L2. The apparent difference in the timing of the L2 EMG from the pattern in the T segments coincides with previous observations that the gross vertebral anatomy[16–18] and spinal kinematics[5,6] are markedly different between these regions.

Travelling waves of flexion–extension along the back can be seen in illustrations from previous reports and appear to differ in their direction between walking and trotting: a wave of flexion–extension travels in a cranial direction along the back during walking[6,19] and in a caudal direction during trot[3]. The registration analysis from this study statistically considered this phenomenon between segments T14 and L2. The analysis showed no consistent direction of travel of such kinematic waves (Fig. 5), but instead showed a similar pattern to the EMG-phase relations (Fig. 5). The general results showed a wave travelling in a cranial–caudal direction along the T sites with a break occurring at the L site L2 (Fig. 5). The propagation of a wave of flexion–extension along the spine depends on the forces acting on the spine, the distribution of inertial mass along the back and the distribution of elasticity and stiffness in the different vertebral regions[20]. The forces include gravitational, inertial, muscle forces (from many muscles), forces from passive skeletal tissues and forces transmitted from the front and hind limbs. The elasticity and stiffness are a combination of passive components from the spinal column and active components provided by the muscles contracting around the spine. All of these components vary along the length of the back and between the T and L regions, and thus it is to be expected that the waves of flexion–extension follow a complex time course along the spine.

In this study, we use the novel application of correlation and registration analysis to the EMG intensities recorded from multiple sites on the *longissimus dorsi*. The results showed distinct patterns of correlation between the left and right sides and shifts in timing of the EMG between different muscle segments and for different locomotor conditions. These results demonstrate that the mechanical function of the *longissimus dorsi* should not be considered as a general property that is applicable to the whole muscle, but instead varies between segments, between locomotor conditions and is under the control of the central nervous system. More detailed assessment of the muscle function will require an understanding of how the muscle fascicle strains vary through the muscle during locomotion, and this in turn will require a detailed understanding of the three-dimensional muscle fascicle geometry. The challenge for future investigations will be to integrate anatomical and *in vivo* measures to relate muscle activity and fascicle strains to locomotor function.

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